Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs

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The shape of the stock-recruitment function does much to determine the form of the equilibrium yield and SSB curves. In order to investigate the sensitivity of the predictions to the fitted curve, we also fitted Ricker[9] and Beverton–Holt[4] curves to the stock-recruitment data and calculated the fishing mortality at which the stock would be expected to collapse (Table 1). The values ranged from 0.91 to 1.13 compared with the estimated current fishing mortality of 0.91. This suggests that the conclusion that the stock is being fished at dangerous levels does not depend on the shape of the stock-recruitment function. The main effect of the choice of different recruitment curves is on the location of MSY. In the case of the Beverton–Holt curve, MSY is located at much lower fishing mortality rates and hence would be a safer exploitation strategy under this assumption. However, the estimated spawning stock at MSY is implausibly large, being a factor of six above the largest ever observed value and corresponds to a fishing mortality rate below any observed historical value.

A particular concern with cod is the pattern of exploitation with age. Cod can live many years and only reach maturity in significant numbers by the age of four. However, fish are caught as early as age one and by age two young fish are fully exploited by the fishery[10]. This means fish suffer substantial fishing mortality before they have a chance to reproduce. At present exploitation rates, only four per cent of fish aged one will survive to the age of four. This is the main reason for the steepness of the slope of the replacement line in Fig. 1b, which characterizes the low survival of recruits into the spawning stock.

Without a substantial reduction in the rate of fishing, the North Sea cod stock may well collapse. Overfishing has caused severe reductions in cod stocks in the northeast Arctic[11], Iceland[12] and Canada[2,3]. Governments have taken severe management actions to help rebuild these stocks, by reducing the total allowable catch or closing fisheries completely. For many years, ICES has advised that the fishing mortality rate for North Sea cod should be reduced but data suggest management efforts have not been effective. There is now an urgent need to ensure that the exploitation rate is reduced either through the use of effective catch controls or by a direct reduction in fishing activity. □

Table 1 The results of fitting three different stock-recruitment functions to North Sea cod data

Function	Shepherd	Ricker	Beverton–Holt
Formula	$R = aS[1 + (S/b)^c]^{-1}$	$R = aS\exp(-bS)$	$R = aS[1 + S/b]^{-1}$
Parameter estimates (s.d.)	a = 3.026 (0.523) b = 248.72 (35.58) c = 3.24 (1.958)	a = 4.151 (0.814) b = 0.0039 (0.0011)	a = 4.900 (1.781) b = 127.37 (86.30)
Coefficient of determination	0.255	0.234	0.215
F_{crash}	0.91	1.05	1.13
F_{msy}	0.77	0.65	0.24
S_{msy}	203	298	1,736

R is recruitment and S is spawning-stock biomass. The quantities a, b and c are equation constants. (a is the slope of the curve at the origin, and the constants b and c determine the curvature in the shock-recruitment relationship). The standard deviation of the estimated parameters is given in parentheses. F_{crash} is the fishing mortality where the equilibrium spawning stock is zero. F_{msy} is the fishing mortality at maximum sustainable yield and S_{msy} is the equilibrium spawning stock at F_{msy} given in thousands of tonnes.

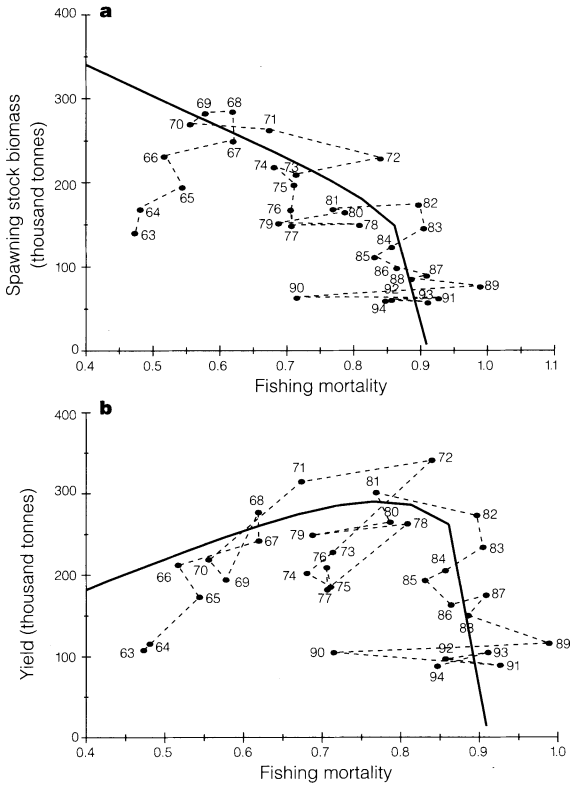

Figure 2 a, The equilibrium spawning stock biomass estimated from the stock-recruitment function fitted in Fig. 1b and the present exploitation pattern as a function of total fishing mortality. The plotted points are the observed values from the most recent assessment joined as a time series. **b**, The equilibrium yield estimated in the same way as **a**. The plotted points are the observed catches plotted as a time series. Both figures show the observed SSB and catch declining in line with the expected equilibrium function.

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Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs

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Young Seychelles warblers *Acrocephalus sechellensis* often remain in their natal territories as helpers. Helpers on low-quality territories (as measured by food availability) reduce their parents' reproductive success, whereas 1–2 helpers on high-quality territories increase their parents' reproductive success, thereby

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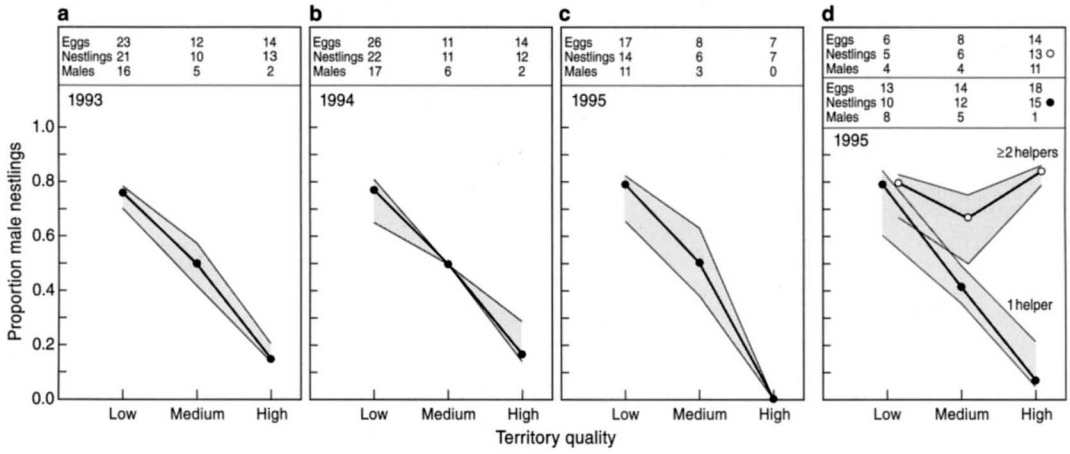

Figure 1 Sex ratio in Seychelles warbler nestlings. **a**–**c**, Sex ratio of nestlings produced by Seychelles warbler pairs in relation to quality class of breeding territory (*tq* classes: 1, low-quality territory; 2, medium-quality territory; and 3, high-quality territory; 1993–1995). No additional young were present on the territory. Young were hatched from one-egg clutches only in different years (**a**, 1993; $n = 46$, *G*-test of independence: $D = 12.23$, d.f. = 1, $P = 0.0005$, proportion male $= 1/(1 + e^{-z})$, $z = -2.68 + 1.36(tq$ class); **b**, 1994: $n = 45$, $D = 12.03$, d.f. = 1, $P = 0.0005$, $z = -2.68 + 1.37$ (tq class); **c**, 1995: $n = 27$, $D = 12.99$, d.f. = 1, $P = 0.0003$, $z = -3.60 + 2.10(tq$ class)). If in the analysis only young were included that had been hatched from different breeding pairs and different mothers, the pattern of sex ratio of nestlings in relation to territory quality class remained the same (1993: $n = 44$, $D = 12.71$, d.f. = 1, $P = 0.0005$; 1994: $n = 34$, $D = 11.71$, d.f. = 1, $P = 0.0006$; 1995: $n = 27$, $D = 12.99$, d.f. = 1, $P = 0.0003$). **d**, Sex ratio of nestlings produced by Seychelles warbler pairs in relation to quality of breeding territory and to the number of helpers present (1995). ($D(tq$ class) = 13.26, d.f. = 1, $P = 0.0003$; D(helper) = 10.86, d.f. = 1, $P = 0.001$; $D(tq$ class x helper) = 11.77, d.f. = 1, $P = 0.0006$; $z = -4.77 + 3.09(tq$ class)+ 1.93(helper) − 1.59(tq class x helper)). Shaded area represents the maximal and minimal values for the sex ratio assuming that all eggs hatched were male, or females, respectively.

enhancing their inclusive fitness, in addition to gaining experience[1,2], and opportunities for co-breeding[3]. Helpers are mostly females, and we have previously suggested that parents may adjust the sex of their single egg to territory quality[4]. We therefore took blood samples from nestlings, and determined sex using random amplified polymorphic DNA (RAPD) markers. We show that biased hatching sex ratios are caused by biased production and not by differential embryo mortality. Unhelped breeding pairs on low-quality territories produce 77% sons, whereas unhelped pairs on high-quality territories produce 13% sons. Breeding pairs that were transferred from low- to high-quality territories switched from the production of male to female eggs. Breeding pairs occupying high-quality territories switched from producing female eggs when no or one helper was present, to producing male eggs when two helpers were present in the territory.

Until 1988, the world population of the endemic Seychelles warbler was entirely confined to Cousin Island (29 ha), where it has reached carrying capacity of about 320 birds[5,6]. The warbler is insectivorous, gleaning insect food from leaves, and usually has a one-egg clutch (91.0%, $n = 223$) once per year and has a high annual adult survival (81.1%, 334 bird-years). The breeding pair remains in the same territory, sometimes for as long as nine years. Although warblers can breed successfully in their first year, some individuals remain on their natal territories as helpers, providing nourishment to their parents' offspring[1–4]. Helpers are mainly females (88%, $n = 271$), which remain significantly longer in their natal territories than males (3.3 and 1.2 years, respectively)[4]. The frequency of helping is affected by habitat saturation and variation in territory quality[5,6], measured in terms of insect prey density. Both territory quality and the presence of helpers are important factors affecting the fitness of parents. Breeding pairs that were transferred from low- to high-quality territories improved their reproductive success significantly[7]. Removal experiments showed that the presence of 1–2 helpers in high-quality territories enhanced the reproductive success of their parents, due to helping behaviour, whereas the presence of helpers on low-quality territories and the presence of 3 or more helpers on high-quality territories decreased future reproductive output of their parents owing to food competition[1]. Here we assess whether warblers are capable of adjusting the sex of their eggs to the quality of the territory they inhabit and, in addition, to the number of helpers already present on the natal territory.

In the three years 1993–95, the fraction of male nestlings produced by unhelped breeding pairs changed significantly with territory quality (Fig. 1a–c). On average, most of the nestlings in low-quality territories were males (77.2%, $n = 57$). Neither sex predominated significantly in medium-quality territories (55.2% males, $n = 27$), and nestlings in high-quality territories were mainly females (87.5%, $n = 32$). The observed hatching sex ratio is not caused by differential embryo mortality. Even if we assume that the few unhatched eggs were of the minority sex in each case, a significant decrease in male nestlings with territory quality still remains (Fig. 1a–c).

The translocation of Seychelles warblers to the previously unoccupied islands of Aride (68 ha) and Cousine (26 ha) in September 1988 and in June 1990, respectively[8,9] allowed us to test experimentally whether individuals indeed modify sex ratio of their clutch in relation to territory quality. Breeding pairs that were transferred from low-quality territories on Cousin to high-quality territories on the new islands, switched from a sex ratio biased towards male eggs before the transfer to mainly female eggs after the transfer (Table 1). Sex ratio of eggs laid by pairs breeding on high-quality territories before and after translocation were biased towards female eggs during both periods (Table 1).

Nestling sex ratio for pairs with one helper was not significantly different from that of pairs with no helpers, and again was negatively associated with territory quality (Fig. 1d). In contrast, pairs with two or more helpers produced mainly sons, even in territories with a high habitat quality (fraction of males, 0.85 ($n = 13$); Fig. 1d). Even if we assume that the unhatched eggs were of the same sex, the biased hatching sex ratio still remains (Fig. 1d). The sequence of egg sex ratio in successive broods in three consecutive years of the same pair in relation to the number of helpers present differed with habitat quality. The production of excess male eggs by pairs on low-quality territories was independent of the number of helpers present

Table 1 Comparison of sex ratios of eggs and territory quality (*tq*) class of Seychelles warbler pairs on Cousin Island before translocation, and of the same pairs on the islands of Aride and Cousine after translocation

	Before translocation Cousin			After translocation Aride, Cousine		
	Low			High		
tq class pair	Daughters	Sons	χ^2(d.f. = 3)	Daughters	Sons	χ^2 (d.f. = 3)
1	0	6		12	0	
2	1	2		3	1	
3	1	6		9	2	
4	0	4		5	2	
Total	2	18	13.90**	29	5	18.76***
	High			High		
tq class pair	Daughters	Sons	χ^2 (d.f. = 2)	Daughters	Sons	χ^2 (d.f. = 2)
5	4	1		2	1	
6	6	2		8	1	
7	5	1		6	2	
Total	15	4	6.47*	16	4	8.11*

The difference between the changes in sex ratios of eggs of the two groups, originating from low- and high-*tq* classes was significant (*G*-test of independence: $D = 20.85$, d.f. = 1, $P < 0.0005$). $*P < 0.05$, $**P < 0.025$, $***P < 0.001$.

Table 2 The sex ratio (proportion male eggs) in successive clutches of the same pairs in relation to territory quality and number of helpers present

Year	1993	1994	1995	No. of	χ^2
Sequence of nestling production	First	Second	Third	pairs	(d.f. = 2)
With helpers in '94–95					
Numbers of helpers	0	1	2		
Hatching sex ratio 1qt	1.00	1.00	0.80	5	2.05
Hatching sex ratio hqt	0.00	0.14	0.71	7	10.42*
Without helpers in '93–'95					
Number of helpers	0	0	0		
Hatching sex ratio 1qt	0.83	0.83	1.00	6	1.14
Hatching sex ratio hqt	0.20	0.00	0.00	5	2.05

All the eggs produced by these pairs resulted in a nestling, which was blood-sampled and sexed using RAPD markers. Abbreviations: lqt: low-quality territory; hqt: high-quality territory. $*P < 0.01$

(Table 2). In contrast, pairs on high-quality territories with no or one helper present produced mainly female eggs, but shifted sex ratio of their eggs to males when two helping offspring were present (Table 2). The third egg produced by pairs on high-quality territories was male when the first two offspring remained as helpers, but female when the first two offspring dispersed from the territory.

The removal of helpers on high-quality territories in June 1990[1] allowed us to test experimentally whether individuals indeed modify sex ratio of their clutch in relation to the number of helpers present. All the eggs laid by six groups during the breeding season before and during the breeding season after the removal of helpers produced nestlings, which survived to be blood-sampled in 1993 for RAPD sexing. Before helper removal, the six eggs laid by the six experimental units comprising the breeding pair with two helpers were all males; after removal of one helper, one son and five daughters were produced (Fisher exact test: $P = 0.007$). The sex ratio of the clutch laid by the reduced groups was exactly the same as that in six control units comprising the breeding pair and one helper (one son, five daughters, both in 1990 and 1991). The difference between the changes in sex ratio of eggs of the two groups, originally with different number of helpers present was significant (*G*-test of independence: $D = 5.98$, d.f. = 1, $P < 0.025$). Seychelles warblers adjust primary sex ratio facultatively in response to the quality of the territory they inhabit and to the number of helpers present on the breeding territories.

In contrast to the small variations in offspring sex ratios that seem to characterize most bird species[10–14], the Seychelles warbler on Cousin Island shows extreme skews in hatching sex ratios. The sex ratio variation in Seychelles warblers offers support for local resource enhancement (LRE) through helping by one sex ('production-of-helpers' hypothesis)[11,15–18]. When helpers enhance the fitness of their parents, warbler breeding pairs produce predominantly the helping female sex. The sex ratio variation in the warblers is further consistent with the local resource competition (LRC) hypothesis[17,18]. By biasing offspring sex ratio towards sons, which disperse, in low-quality territories and daughters in high-quality territories, breeding birds avoid having competing offspring on low-quality territories (LRC), and gain helpers on high-quality territories (LRE). With three or more helping birds present in a high-quality territory, the reproductive success of the parents decreases, resulting from increased risk of egg break caused by simultaneous incubation by four or more females, and greater depletion of food resources[1,3]. When two adult helping young were already present in high-quality territories, individual breeding pairs shifted from producing daughters to producing sons. Seychelles warblers increase their fitness by adaptively modifying the primary sex ratio. These results support the general proposition that sex ratio variation is expected when the profitabilities of raising sons or daughters very between individuals[19]. To our knowledge, the Seychelles warbler is the first species in which future benefits accruing to the parents have been shown to contribute to the evolution of adaptive sex ratio manipulation. □

Methods

Data collection. On Cousin, all 115–123 breeding groups (310–400 birds) were checked regularly (every two weeks in 1985–1991; every four weeks in 1992–1996) for breeding activity from December 1985 to August 1996. Data were based on individually colour-ringed birds. As warblers have never colonized other islands by themselves, we assumed that missing birds had died if they were not found on other territories. Nestlings between 4 and 12 days old

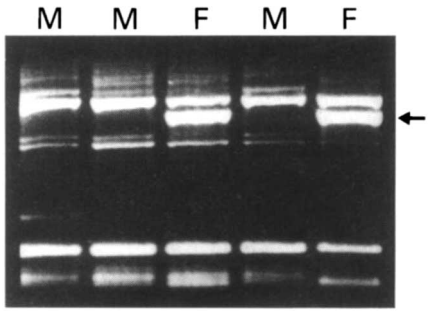

Figure 2 PCR products from genomic DNA of Seychelles warblers showing a female-specific fragment of 1.02 kb (indicated by an arrow; M, male; F, female).

and adults were blood-sampled in 1993–95 for sexing using RAPD markers. All nests were checked for the presence of a clutch, and clutch size during the 3–5 days after laying the first egg. In the analyses, only one-egg clutches were included, because these eggs were certainly from the breeding pair[20]. From 1993 to 1995, all nestlings produced within a 5-week period, the main breeding season, by breeding pairs without helpers were sampled. Most of the nestlings born in the population hatched during this 5-week period (82.0%, $n = 273$)[7]. In 1995, all nests built within a 5-week period by all breeding groups, including those with helpers on Cousin were checked for a clutch, and all nestlings produced within this period were blood sampled.

A total of four breeding pairs from low-quality territories and three breeding pairs from high-quality territories on Cousin were transferred to Cousine and Aride[8,9]. On the new islands they remained paired and occupied high-quality territories. All the eggs produced by these pairs pre- and post transfer resulted in a nestling, which survived to be blood-sampled in 1993 and sexed using RAPD markers.

Territory quality. Territory quality was expressed as mean insect prey available within a territory, because adult survival and reproductive success correlated with this[3,6]. Territory quality was measured each month, and calculated as $tq = a\sum_{x=1}^{12}(c_x i_x))/100/\Sigma$ where a is the mean yearly territory size (hectares), c_x is the mean yearly foliage cover for plant species x, and i_x is the mean monthly insect totals for plant species x per square decimetre of leaf area per year. Territories were divided into three classes: class 1 is low ($tq = 0$–$1{,}500$), class 2 is medium ($tq = 1{,}501$–$3{,}000$), and class 3 is high quality ($tq > 3{,}000$).

Sex determination. DNA was extracted[21] from blood samples (10–50 μl) collected from 4–12-day-old nestlings by brachial venipuncture. Amplification consisted of 38 cycles with primer 5′-GGGTAACGCC-3′ according to ref. 22 and the products were separated on a 1.5% agarose gel. The PCR products from genomic DNA of all nestlings were scored blindly for the presence of the female-specific fragment by two uninformed persons (Fig. 2). In cases of disagreement, the analysis was repeated. All males ($n = 98$) and females ($n = 86$) seen copulating at a later stage were correctly sexed by this method.

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Female infertility in mice lacking connexin 37

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The signals regulating ovarian follicle development and the mechanisms by which they are communicated are largely undefined[1]. At birth, the ovary contains primordial follicles consisting of meiotically arrested oocytes surrounded by a single layer of supporting (granulosa) cells. Periodically, subsets of primordial follicles undergo further development during which the oocyte increases in size and the granulosa cells proliferate, stratify and develop a fluid-filled antrum. After ovulation, oocytes resume meiosis and granulosa cells retained in the follicle differentiate into steroidogenic cells, forming the corpus luteum[1,2]. It has been proposed that intercellular signalling through gap junction channels may influence aspects of follicular development[3,4]. Gap junctions are aggregations of intercellular channels composed of connexins, a family of at least 13 related proteins that directly connect adjacent cells allowing the diffusional movement of ions, metabolites, and other potential signalling molecules[5]. Here we show that connexin 37 is present in gap junctions between oocyte and granulosa cells and that connexin-37-deficient mice lack mature (Graafian) follicles, fail to ovulate and develop numerous inappropriate corpora lutea. In addition, oocyte development arrests before meiotic competence is achieved. Thus, cell–cell signalling through intercellular channels critically regulates the highly coordinated set of cellular interactions required for successful oogenesis and ovulation.

Immunocytochemistry was performed on frozen sections of mouse ovaries to investigate the composition of oocyte–granulosa cell gap junctions. Antibodies specific for connexins (Cx) 37, 40 and 43 were used because their messenger RNAs had been previously detected in ovary[6–8]. Anti-Cx37 antibodies[9] labelled oocyte surfaces with a punctate staining pattern both in developing (Fig. 1a, b; 100 out of 100 cases) and in Graafian follicles (Fig. 1c, d; 30 out of 30 cases) but not primordial follicles (data not shown). This is consistent with the known location of oocyte–granulosa cell gap junctions[3]. Anti-Cx40 antibodies did not label ovarian follicles (data not shown). Antibodies to Cx43 labelled granulosa–granulosa gap junctions as expected[6] but in contrast to anti-Cx37 antibodies, did not label the surface of the oocyte (Fig. 1g, h). Although low levels of Cx43 immunoreactivity in oocytes have been reported[6,10], our results indicate that Cx43 does not contribute significantly to oocyte–granulosa junctions and that Cx37 is the predominant oocyte connexin.

Uniform female infertility was observed when a targeted mutation in the Cx37 gene (Fig. 2a) was generated to test the role of intercellular communication in follicle development. Heterozygous ($Cx37^{+/-}$) mice, which appeared grossly normal, were interbred and the resulting litters genotyped by Southern blotting or polymerase chain reaction (PCR) (Fig. 2b). The ratio of genotypes was mendelian (1:2:1), indicating that there was no reduction in